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DIVERSIFIED GERMINATION BEHAVIOR OF *PARKINSONIA MICROPHYLLA* (FOOTHILL PALOVERDE, FABACEAE)

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Abstract

Diversified germination behavior has been well documented for winter annuals in the Sonoran Desert but has been reported for few woody plants in the region. Despite a long-held assumption that seeds of the leguminous tree *Parkinsonia microphylla* (foothill paloverde) are impermeable to water until scarified by natural abrasion, a variable proportion can germinate shortly after dispersal without scarification. Seed crops thus comprise nondormant as well as dormant seeds and exhibit diversified germination behavior. Under controlled conditions (25°C), germination of unscarified seed averaged 32%. Under natural rainfall regimes, germination of unscarified seed ranged from 4% to 49%. Laboratory experiments suggest that permeability of fresh seed is highest under warm temperatures and no more than a single cycle of wetting and drying. Diversified germination behavior has profound implications for population dynamics. In the case of *P. microphylla,* the mixture of dormant and nondormant seeds promotes multiple pulses of germination each summer and ensures coordination between cohort size and soil moisture levels.

Resumen

Diversificación en comportamiento de germinación ha sido bien documentado para anuales invernales pero poco para plantas leñosas del Desierto Sonorense. A pesar de la suposición que las semillas de *Parkinsonia microphylla* son impermeables antes de ser escarificadas, una proporción variable de semillas pueden germinar sin escarificación siguiente a dispersión. Por lo tanto la producción anual de semillas incluye semillas aletargadas y no aletargadas cuales manifestan diversificación en comportamiento de germinación. Bajo condiciónes controladas, un promedio de 32% de las semillas se germinaron a 25°C. Con un régimen natural de lluvia, se germinaron entre 4% y 48% de las semillas no escarificadas. Experimentos indican que la permeabilidad de semillas nuevas es mas alta con temperaturas cálidas y no mas que un ciclo de humedad y sequía. Diversificación en el comportamiento de germinación tiene consecuencias profundas para la dinámica de poblaciónes. En el caso de *P. microphylla* la mezcla de semillas aletargadas y no aletargadas promueve múltiple pulsos de germinación cada verano y asegura la coordinación entre el tamaño del cohorte de semillas y el nivel de la humedad del suelo.

Key Words: Climatic variability, seed dormancy, seed permeability, Sonoran Desert.

Diversified germination behavior, in which seeds from a single crop display different levels of dormancy, has profound implications for population dynamics. It is well known that winter annuals in the Sonoran Desert employ this strategy (Westoby 1981; Venable and Pake 1999), but diversified germination behavior has been reported for few woody plants in the region. Here I report on diversified germination of *Parkinsonia microphylla* Torrey, a drought-deciduous, leguminous tree common in the Sonoran Desert of Arizona and northern Mexico.

Parkinsonia microphylla flowers in late April and May and disperses seed in June. Dispersal agents include scatter-hoarding sciurid (personal observation) and heteromyid (McAuliffe 1990) rodents that bury the seeds at depths of 2 to 3 cm. Dormant seeds remain in the soil and, if not destroyed by predators or pathogens, germinate over the next several years (Shreve 1951; McAuliffe 1990; Bowers 1994). Seeds germinate in response to summer (July to October) rains $\geq$ 17 mm (Bowers 1994). A single cycle of wetting and drying lowers germination by 50% (Poole 1958). Given adequate summer rain, seedlings are usually plentiful (Shreve 1917; Bowers and Turner 2002). New seedlings are highly vulnerable to predation (McAuliffe 1986; Bowers and Turner 2002) and, to a lesser extent, seasonal drought (Shreve 1917; Bowers and Turner 2002).

Some Sonoran Desert ecologists have long assumed that the hard seeds of *P. microphylla* are impermeable to water and will not germinate until scarified by natural abrasion (e.g., Shreve 1951; Turner et al. 1995), an assumption based on laboratory trials in which germination required mechanical or chemical scarification. If hard seeds will not germinate without scarification, it is safe to assume that they are dormant. Germination of unscarified *P. microphylla* seed has been reported several times but not ascribed any particular importance. In one study, < 2% of unscarified seeds germinated (McAuliffe 1990); in another, high germination (88%) was inconsistently attributed to permeable seed coats or scarification of stored seed by insects (Poole 1958). Barton (1947) found that 10% of untreated seeds imbibed water (and could presumably germinate) but did not discuss this finding.

Two observations made at Tumamoc Hill, Tucson, Arizona, suggest that despite previous assumptions, *P. microphylla* seed crops might comprise dormant and nondormant seeds. First, in spring 2002, I observed that *P. microphylla* did not flower at Tumamoc Hill after severe winter drought, and there was no seed crop. Nevertheless, 40 seedlings emerged on Area A, a 557-m^2 plot on Tumamoc Hill, following adequate rains in July. The following winter was also very dry, and again *P. microphylla* failed to flower on Tumamoc Hill. After germinating rains in August 2003, there were 11 new seedlings on Area A. The emergence of seedlings after two years of crop failure confirms the existence of a between-year seed bank (McAuliffe 1990) and indicates that some seeds are dormant. Second, after summer rains in August 1997, I observed emergence of *P. microphylla* seedlings at a second site near Tucson, Arizona. Seedlings emerged in tight clusters as if from rodent caches (McAuliffe 1990). Because the soil had been thoroughly dug and turned the previous winter, these seeds must have been cached soon after they ripened in June 1997; if so, they were no more than two months in age at the time of germination. Evidently, a proportion of the seed crop can germinate in the year of dispersal and is nondormant.

Taken together, these observations suggest that *P. microphylla* displays diversified germination behavior. This study used germination experiments under controlled and natural conditions to confirm that seeds can indeed germinate in the year of dispersal, to determine what proportion of the seed crop is nondormant, and to learn whether this proportion changes in response to environmental factors such as temperature or cycles of wetting and drying.

METHODS

Study Sites

Observations reported above were made at the Tumamoc Hill and Ruthann Road sites; outdoor germination experiments were conducted at the Ruthann Road site. The Tumamoc Hill site is a 352-ha nature preserve and research station just west of downtown Tucson, AZ (32°13′N, 111°05′W). Elevations range from 725 to 948 m above sea level. The Ruthann Road site is just northwest of Tucson at 720 m above sea level. Although this site is in a residential area, housing density is low, and much natural vegetation has been preserved. The sites are about 11 km apart and support vegetation typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). Native birds, rodents, lagomorphs, canids, and other wildlife are abundant at both sites. At Tucson, rainfall averages 280 mm per yr. Almost half comes during July, August, and September; most of the remainder falls between November and March (Sellers et al. 1985). Average maximum and minimum daily temperatures are 18.6°C and 2.4°C during January, the coldest month, and 37.9°C and 22.8°C in June, the hottest month (Sellers et al. 1985). In June and early July, daily soil temperatures at a depth of 7.5 cm commonly fluctuate between 25°C and 52°C (Shreve 1931).

Germination under Natural Conditions

Two experiments were conducted under natural conditions to confirm that *P. microphylla* seeds can indeed germinate in the year of dispersal. Ripe seeds were harvested from several trees on June 15, 2001, and divided into eight replicates of 20 seeds each. Half the replicates were scarified by rubbing the seed coats with a metal file. On June 18, 2001, a shallow trench approximately 4 cm × 100 cm × 200 cm was dug in dry desert soil. Eight cylindrical cages made of narrow-mesh (6.4 mm) hardware cloth were placed in the trench; the cages were about 14 cm high and 36 cm in diameter. Replicates were randomly assigned to cages. Seeds were placed in a single layer on the ground within each cage, then covered with soil to a depth of about 2.5 cm. The trench was backfilled so that its surface was flush with the soil in the cages. To protect seeds from animals, cages were covered with lids of hardware cloth weighted down by rocks. Germination in response to summer rains was recorded from July to September 2001.

The experiment was repeated with some modifications two years later. Ripe seeds were harvested on June 15, 2003, and divided into four replicates of 25 seeds each. A razor blade was used to nick all seeds in two replicates. Seeds were sown in desert soil in four plastic nursery flats (32.5 cm × 32.5 cm × 7.5 cm) at a depth of 2.5 cm on June 17, 2003. Flats were placed in a shallow trench in the ground, then the trench was backfilled until the soil surface was flush with the top of the flats. A wire screen was placed over the flats to protect seeds from birds and rodents. Again, germinations were recorded throughout the summer. Ungerminated seeds were retrieved at the end of the experiment and scarified with a razor blade, whether previously scarified or not. Seeds were pooled within treatments, then placed on moist filter paper in Petri dishes, sealed inside small, transparent plastic bags, and germinated at room temperature (25°C).

Germination under Controlled Conditions

Seeds used in the following experiments were harvested from trees on June 22, 2003, and stored in small lots in Petri dishes at room temperature (25°C) until use. Scarified seeds were treated by nicking the seed coat with a razor blade. All seeds were germinated or incubated on moist filter paper in Petri dishes that were individually sealed inside small, transparent plastic bags. Distilled water was added as necessary to maintain an even moisture level. During germination or incubation, seeds were

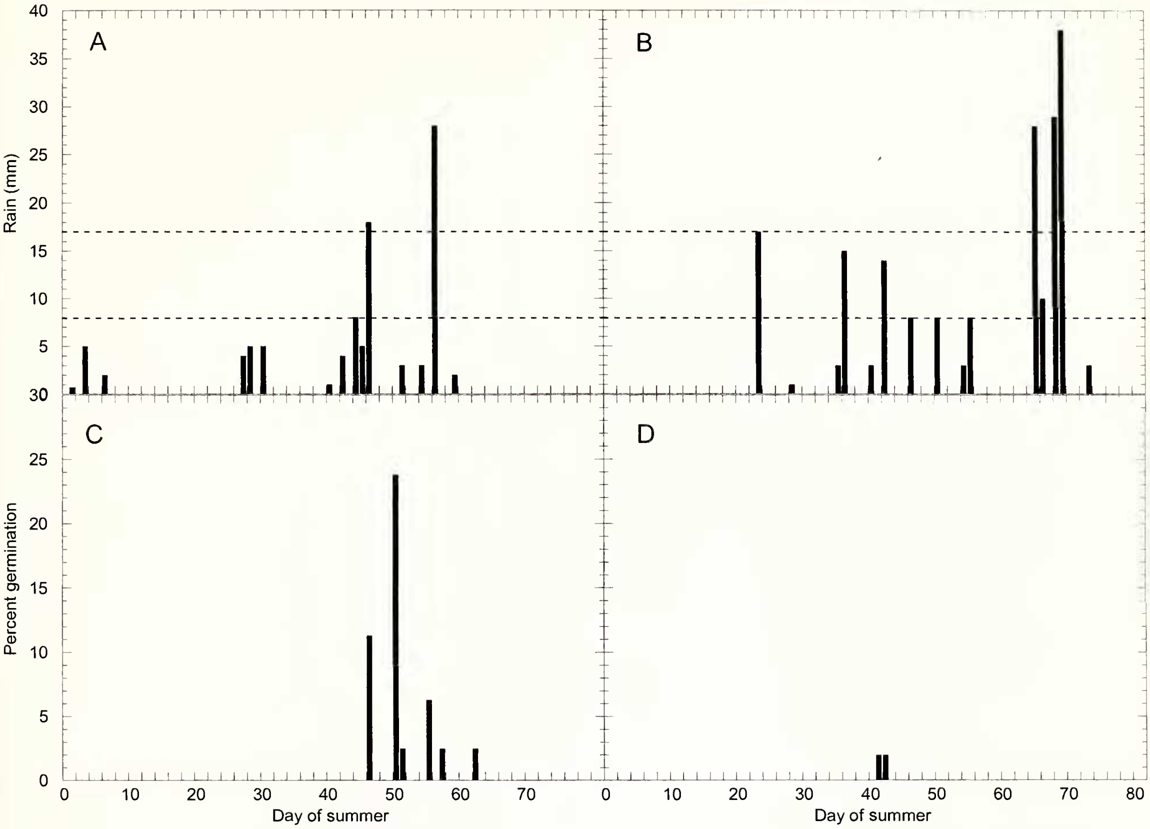

FIG. 1. Germination of unscarified *Parkinsonia microphylla* seed under natural conditions in 2001 and 2003. Scarified seeds not shown. On the X axis, days are numbered consecutively from June 20 to September 6. Dashed lines represent the 17-mm threshold for germination and the 8-mm threshold for effective precipitation at a depth of 2 to 3 cm. (A) Summer rain (mm) in 2001, Tucson, Arizona. (B) Summer rain (mm) in 2003, Tucson, Arizona. (C) Percent germination in 2001 (N = 80 seeds, replicates pooled). (D) Percent germination in 2003 (N = 50 seeds, replicates pooled).

kept at constant temperatures in an incubation chamber (40°C) or in a temperature-controlled room (25°C). Germination of *P. microphylla* is essentially indifferent to light (Poole 1958); therefore, seeds were maintained at ambient light levels, about 12 hr day/night.

To determine viability of fresh seed, scarified and unscarified seeds were germinated at 25°C in four separate trials. Seeds ranged in age from five days in the first trial to 64 d in the last. For each treatment there were two replicates of 25 seeds each. Germination was monitored for eight days.

The effect of wetting followed by drying was tested with seeds that were 75 d of age at the start of the experiment. Seeds were subjected to zero, one, three, or five cycles of wetting and drying at 25°C or 40°C. There were two replicates of 25 seeds each for every treatment. For each wetting/drying cycle, seeds were incubated in covered Petri dishes on moist filter paper at 25°C or 40°C for 24 hr, then placed in uncovered Petri dishes on dry filter paper and kept for four days at the same temperature as before. These parameters reflected moisture and temperature conditions typical of the summer rainy season. At the end of one, three, or five wetting/drying cycles, seeds were germinated without delay at 25°C for five days. Seeds given zero wetting/drying cycles were germinated at 25°C or 40°C for five days. The short germination period approximated the brief duration of soil moisture after summer rains. Analysis of variance was used to determine the effect of number of cycles and temperature on percent germination. Before analysis, percents were arcsine-transformed to more closely approximate a normal distribution. Percent germination was calculated after adjusting sample size to correct for any seeds that germinated during the treatment phase.

RESULTS

Germination under Natural Conditions

In 2001, summer rains began in late June but no single storm was large enough to trigger germination (≥17 mm) until the beginning of August, when 30 mm of rain fell over three days (Fig. 1a). Emergence of unscarified seed was first observed on August 6 and continued intermittently through August

20 in response to additional storms (Fig. 1c). Mean germination for scarified and unscarified seeds was 17.5% (SD = 31.8%) and 48.7% (SD = 12.5%), respectively. The means were not significantly different in a t-test using arcsine-transformed values ($t = 1.7$, $P = 0.16$). Variables were transformed before analysis to approximate a normal distribution. The poor germination of scarified seeds was unexpected and suggested that many seeds were incompletely scarified.

In 2003, summer rains started in mid-July (Fig. 1b). The first storm reached the 17-mm threshold but did not trigger germination of unscarified seed. Some scarified seeds did germinate in response to this rain. The next substantial storm, 15 mm on July 25, triggered germination of two unscarified seedlings on July 30 and 31 (Fig. 1d); evidently the storm was not heavy enough to bring about mass germination. Successive rains were frequent but light until a rain of 28 mm on August 23. No unscarified seeds emerged in response to this storm, nor to storms totaling 67 mm on August 26 and August 27. Mean germination of scarified and unscarified seeds was 70% (SD = 8.5%) and 4% (SD = 5.7%), respectively, a significant difference ($t = 9.2$, $P = 0.018$). Ungerminated seeds retrieved at the end of the experiment were highly viable; after scarification, germination averaged 88% for previously untreated seeds and 100% for previously scarified seeds.

Germination under Laboratory Conditions

During four trials, mean germination of scarified seed ranged from 86% to 98% and of unscarified seed from 20% to 50%. The mean of means was 91.5% (SD = 5.0%) for scarified seed, 32.0% (SD = 12.4%) for unscarified seed. Because scarified seed germinated to a high percentage, it appears that most if not all seeds were viable; therefore, failure of unscarified seeds to germinate can be ascribed to dormancy rather than poor viability. During germination, unscarified seeds darkened first at the hilar end, suggesting that water entered through the micropyle, hilum, or lens. Carefully controlled experiments will be needed to determine the exact point of water entry.

Mean germination after zero, one, three, and five wetting/drying cycles was 26.0%, 24.0%, 4.0%, and 6.8% for seeds incubated at 25°C, and 51.0%, 18.5%, 10.1%, and 5.4% for seeds incubated at 40°C. In ANOVA, number of cycles had a strong effect on percent germination ($F_{(3,8)} = 42.9$, $P < 0.001$), and temperature had a modest effect ($F_{(1,8)} = 7.4$, $P = 0.026$). There was a significant interaction between number of cycles and incubation temperature ($F_{(3,8)} = 9.1$, $P = 0.006$). For seeds that did not undergo wetting and drying, germination was at 40°C was twice that at 25°C. Under either temperature regime, germination declined sharply after one wetting/drying cycle.

Discussion

The results of this study demonstrate that a variable proportion of fresh *P. microphylla* seeds can germinate without scarification. Under controlled conditions, germination of unscarified seed at 25°C ranged from 20% to 34% and averaged 32% (SD = 13.4%). Under natural rainfall regimes, germination of unscarified *P. microphylla* seed showed considerable interannual variability, averaging 49% in 2001 and 4% in 2003.

Seed-coat impermeability is usually a function of lignified palisade cells in the seed coat (Baskin and Baskin 1998; Baskin et al. 2000). Many hard-seeded legumes produce some permeable seeds that can germinate without scarification; the point of water entry is often the micropyle, hilum, or lens (Korban et al. 1981; Agbo et al. 1987; Baskin et al. 2000). In the case of *P. microphylla,* permeability might depend in part on whether the hilar region is completely sealed. In the wetting/drying experiment, germination of untreated seed (zero cycles) was greater at 40°C (51%) than at 25°C (26%), suggesting that warmth influenced permeability in the hilar region. Because germination declined as number of wetting/drying cycles increased, it appeared that patterns of moisture also had a strong effect on permeability. Under natural conditions, patterns of moisture of course depend on rainfall. To moisten buried *P. microphylla* seeds, rains must penetrate to a depth of about 2 to 3 cm, the depth at which rodents bury seeds (McAuliffe 1990). On Tumamoc Hill, light rains (<8 mm) have little effect on percent soil moisture at this depth (Shreve 1914, 1934) and are probably not involved in natural wetting/drying cycles. In 2001, there was only one storm ≥ 8 mm before germinating rains fell in early August, so buried seeds experienced no more than a single cycle of wetting and drying. In 2003, there were six storms of this magnitude before germinating rains in late August and therefore six cycles of wetting and drying. Thus, in nature as well as in the laboratory, good germination of unscarified seed was associated with minimal wetting and drying, poor germination with frequent wetting and drying.

Certain other leguminous trees with hard seeds in the northern Sonoran Desert also might exhibit diversified germination behavior. In laboratory studies, 2% to 12% of seeds of *Parkinsonia florida* (Bentham ex A. Gray) S. Watson imbibed or germinated without treatment (Barton 1947; Poole 1958), indicating that a fraction of the seed crop is nondormant. Similarly, imbibition or germination of untreated *Prosopis velutina* Wooton seeds in three different studies was 6% to 7% (Glendening and Paulson 1955), 18% (Poole 1958), and 30% (Barton 1947). Well before diversified germination behavior became a topic of interest to ecological theorists, Glendening and Paulson (1955) noted that because *Prosopis* seed coats vary in permeability, germination of a cohort likely would be staggered. Under natural conditions, germination behavior of *Prosopis* is further complicated by the hard, leathery pericarp that surrounds the seeds. The pericarp is impermeable to water, preventing germination until it is fractured or split (Glendening and Paulson 1955), a service frequently performed in the wild by heteromyid rodents, especially *Dipodomys* (Cox et al. 1993). The strategy of *Olneya tesota* A. Gray apparently differs somewhat from that of *Parkinsonia* and *Prosopis.* When dispersed in June, *Olneya* seeds are soft and highly germinable (77%) (Poole 1958; see also Shreve 1951), but they require scarification when aged (Went 1957; Emery 1988). The increase in seed-coat hardness with age suggests that timely summer rains should trigger mass germination soon after dispersal, but, if summer rains fail, uneaten seeds should gradually harden, facilitating persistence until the following summer. Further studies are needed to determine whether these species do indeed exhibit diversified germination behavior.

One consequence of diversified germination behavior for *P. microphylla* is multiple pulses of germination and emergence each summer (Bowers 1994; Bowers and Turner 2002). The first pulse might well represent nondormant seeds dispersed earlier that summer; later pulses might comprise older seeds newly released from dormancy. The factors that break dormancy in this species are unknown but as for many other hard-seeded legumes might involve exposure to high or widely fluctuating temperatures (Baskin and Baskin 1998). By distributing risk through time, multiple emergence pulses might increase the probability of establishment. The primary risk is probably predation; the limited data available suggest that most *P. microphylla* seedlings are eaten before they have a chance to die of drought stress (McAuliffe 1986; Bowers and Turner 2002). Another consequence of diversified germination behavior is that, as for winter annuals, the proportion of seeds that germinate varies between years and depends at least in part on environmental factors. Given heavy rain soon after dispersal, seeds germinate to a relatively high percentage. If summer rains are frequent and light, only a small percentage of the seed crop remains nondormant. Thus, cohorts derived from fresh seed are likely to be large when moisture is ample, small when moisture is barely adequate. By ensuring coordination between cohort size and soil moisture, responsiveness to wetting/drying cycles should be an effective strategy for dealing with interannual and spatial climatic variability in the Sonoran Desert. Future investigations could examine the possibility that diversified germination behavior in *P. microphylla* functions as a bet-hedging strategy in which reduction in the fitness of individual generations results in increased fitness over many generations.

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